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The Life Cycle of *Lithobius mutabilis* L. Koch, 1862 (Myriapoda: Chilopoda)

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Abstract. The post-embryonic development and life cycle of *Lithobius mutabilis* L. Koch, 1862 were studied. Data for stage analyses were obtained by laboratory breeding and continuous observations of field-collected specimens in captivity over more than five years. Developmental stages are described with respect to the following characters: number of legs (anamorphic stages only), head length and width, length and width of tergite 3, body length, biomass, number of coxal pores, ocelli, and antennal articles. All characters were measured on living individuals under CO₂-anaesthesia. Information concerning oviposition and egg development, onset of sexual dimorphism and maturity, stage duration and moulting activity, life span and mortality as well as observations on feeding behaviour are provided. The results are compared with those of other investigations on *L. mutabilis* and other lithobiid species.

Keywords. Post-embryonic development, morphological characters, bionomy, Lithobiidae.

1. INTRODUCTION

Centipedes are essential components of the predatory arthropod fauna. Because of their considerable suitability as indicators of ecological site conditions, Lithobiidae attract utmost attention. The use of species as biological indicators is based on the knowledge of its ecofaunistical behaviour, phenology and bionomical strategy. Studies on centipede bionomics are much rarer than those on millipedes. Life cycles and stage morphology are known from only 40 centipede species, among them some 20 Lithobiomorpha, whereas about 150 millipede species have been investigated. For practical reasons, attention should be paid firstly on common and frequent species, like *Lithobius mutabilis* in Central Europe, which plays an important role as a dominant epigaeic predator especially in woodlands. Further, this species has the advantage that its life cycle has already been the subject of studies by ALBERT (1983a, b) and FRÜND (1983) in western Germany (Solling, Steigerwald), using field-collected individuals as well as laboratory breeding. The availability of data on the life cycle of *L. mutabilis* from other localities allows possible similarities and differences in pattern to be investigated. Comparisons are also made with the post-embryonic development of other *Lithobius* species.

Our knowledge on post-embryonic development of myriapods was outlined by VERHOEFF (1905, 1925) with the concepts of “anamorphosis” (moultings connected with increases of body segments and legs), “epimorphosis” (moultings cause only differentiations in certain characters but keep constant numbers of body segments and legs) and “hemianamorphosis” (both developmental pathways

in succession). All Lithobiomorpha develop by hemianamorphosis: a juvenile hatches with a small number of segments and legs and develops by a series of moults. At each moult there is an increase of segments and legs until a defined number is reached (anamorphic development). Further moults only lead to a growth in body size and a modification of various structures without increase of segments (epimorphic development).

This study is mainly focussed on the post-embryonic development (breeding biology, development, attainment of maturity and life span) of *Lithobius mutabilis* L. Koch, 1862. This has been done by laboratory breeding and cultures over several years. Description of stages, of variation in some morphological characters (e.g., number of antennal articles, ocelli, coxal pores) and growth analyses occupies a large part of the present study.

2. MATERIALS AND METHODS

2.1. Field collections

A total of 184 individuals of *L. mutabilis* were collected by hand in a deciduous woodland in the Neiße Valley near Görlitz through all seasons in the course of seven years: (1992) 1993–1997 (1998). The animals were transferred to the laboratory for measurement and further rearing. To ascertain the stage of freshly captured adults, it was sometimes necessary to observe two or more moults to overcome the wide overlap of characters between stages.

2.2. Laboratory rearing

For rearing, I used closed plastic vessels measuring 6 x 12 x 6 cm with a ground-layer of gypsum (no soil or leaf litter). The vessels were kept in a climate chamber at a constant temperature of 16 °C, which is the preferred temperature under natural conditions (BAUER 1955; PFLEIDERER-GRUBER 1986). They were examined every second day (youngest juveniles every day) in order to record all moults and egg-laying or to remove dead or sick individuals. At the same time the animals were fed (with collembolans, pieces of earthworms, enchytraeids, *Tubifex*, and, additionally, green leaf pieces of indoor plants), vessels were cleaned and the gypsum layer was moistened. Normally, two to three field collected or laboratory-bred specimens that were individually distinguishable were kept in one vessel.

Seventy-seven juveniles hatched under laboratory conditions. They were immediately isolated and transferred to other vessels, in order to prevent them from being eaten by the parents.

2.3. Measurements

The following results are based on the analyses of all the material, regardless of whether it was laboratory reared or more or less freshly captured.

Body-length, length and width of head and tergite 3, biomass (total numbers of body measurements see Table 1); numbers of coxal pores, antennal articles and ocelli were measured using a stereo-microscope with 12.8–40 x magnification (at μm -precision) and an analytical balance (precision 0.1 mg), respectively. Dead individuals were not weighed.

All individuals were measured alive under CO_2 -anaesthesia. To check all characters, 3 to 4 gas treatments (each for some seconds only) were necessary. The CO_2 -method has two important advantages: firstly, it is not damaging, i.e., it is possible to follow the development of one individual by measuring it after each moult; secondly, measurements of the relaxed animal can be obtained in contrast to measurements in alcohol, where body parts are contracted or curled up. However, using living material has the disadvantage of restricting measurements to "coarse" characters due to the short anaesthesia period.

3. RESULTS

3.1. Analysis of post-embryonic developmental stages

Designation of stages. In the centipede literature there is still disagreement about counting and nomenclature of the stages defined by the moults. VERHOEFF (1905, 1925) called the 1st juvenile stage a "foetus", the 2nd a "larva prima", "larva secunda", etc. Some authors (e.g., PFLEUGFELDER 1932; DOHLE 1969, 1986) emphasized that the post-embryonic stages of centipedes are not true larvae. They neither have distinct larval characters nor do they live under ecological conditions different from those of the adults. Nevertheless, most of the authors continue

Table 1. Total numbers of measurements taken at different stages (BL – body length, HL – head length, HW – head width, T3L – length of tergite 3, T3W – width of tergite 3, BM – biomass). To be read in conjunction with Figure 1.

| Stage | | BL | HL | HW | T3L | T3W | BM |
|------------|---|------------|------------|------------|------------|------------|------------|
| I | | | | 9 | 8 | 9 | – |
| II | | | | 9 | 7 | 7 | – |
| III | | 34 | 37 | 36 | 34 | 36 | – |
| IV | | 31 | 31 | 31 | 30 | 31 | – |
| V | | 32 | 32 | 32 | 31 | 32 | 11 |
| VI (1) | | 35 | 35 | 35 | 35 | 35 | 26 |
| VII (2) | ♂ | 17 | 18 | 18 | 18 | 18 | 17 |
| | ♀ | 19 | 20 | 20 | 20 | 18 | 14 |
| VIII (3) | ♂ | 14 | 16 | 16 | 16 | 16 | 13 |
| | ♀ | 17 | 17 | 17 | 17 | 17 | 15 |
| IX (4) | ♂ | 16 | 10 | 10 | 10 | 10 | 9 |
| | ♀ | 8 | 9 | 8 | 9 | 9 | 9 |
| X (5) | ♂ | 21 | 30 | 30 | 28 | 28 | 25 |
| | ♀ | 14 | 15 | 15 | 14 | 14 | 13 |
| XI (6) | ♂ | 40 | 44 | 43 | 43 | 43 | 41 |
| | ♀ | 19 | 24 | 24 | 24 | 24 | 23 |
| XII (7) | ♂ | 37 | 46 | 46 | 44 | 45 | 43 |
| | ♀ | 29 | 32 | 32 | 31 | 31 | 28 |
| XIII (8) | ♂ | 25 | 28 | 29 | 29 | 29 | 27 |
| | ♀ | 17 | 21 | 21 | 20 | 21 | 20 |
| XIV (9) | ♂ | 14 | 14 | 14 | 14 | 14 | 14 |
| | ♀ | 12 | 13 | 12 | 13 | 13 | 12 |
| XV (10) | ♂ | 8 | 9 | 9 | 9 | 9 | 8 |
| | ♀ | 13 | 13 | 13 | 13 | 13 | 13 |
| XVI (11) | ♂ | 5 | 5 | 5 | 5 | 5 | 4 |
| | ♀ | 3 | 3 | 3 | 3 | 3 | 3 |
| XVII (12) | ♂ | 3 | 4 | 4 | 4 | 4 | 3 |
| | ♀ | 4 | 4 | 4 | 4 | 4 | 4 |
| XVIII (13) | ♂ | 2 | 2 | 2 | 2 | 2 | 2 |
| | ♀ | 4 | 4 | 4 | 4 | 4 | 4 |
| XIX (14) | ♂ | 2 | 2 | 2 | 2 | 2 | 2 |
| | ♀ | 1 | 1 | 1 | 1 | 1 | 1 |
| XX (15) | ♂ | 1 | 1 | 1 | 1 | 1 | 1 |
| Sum | | 497 | 540 | 555 | 543 | 548 | 405 |

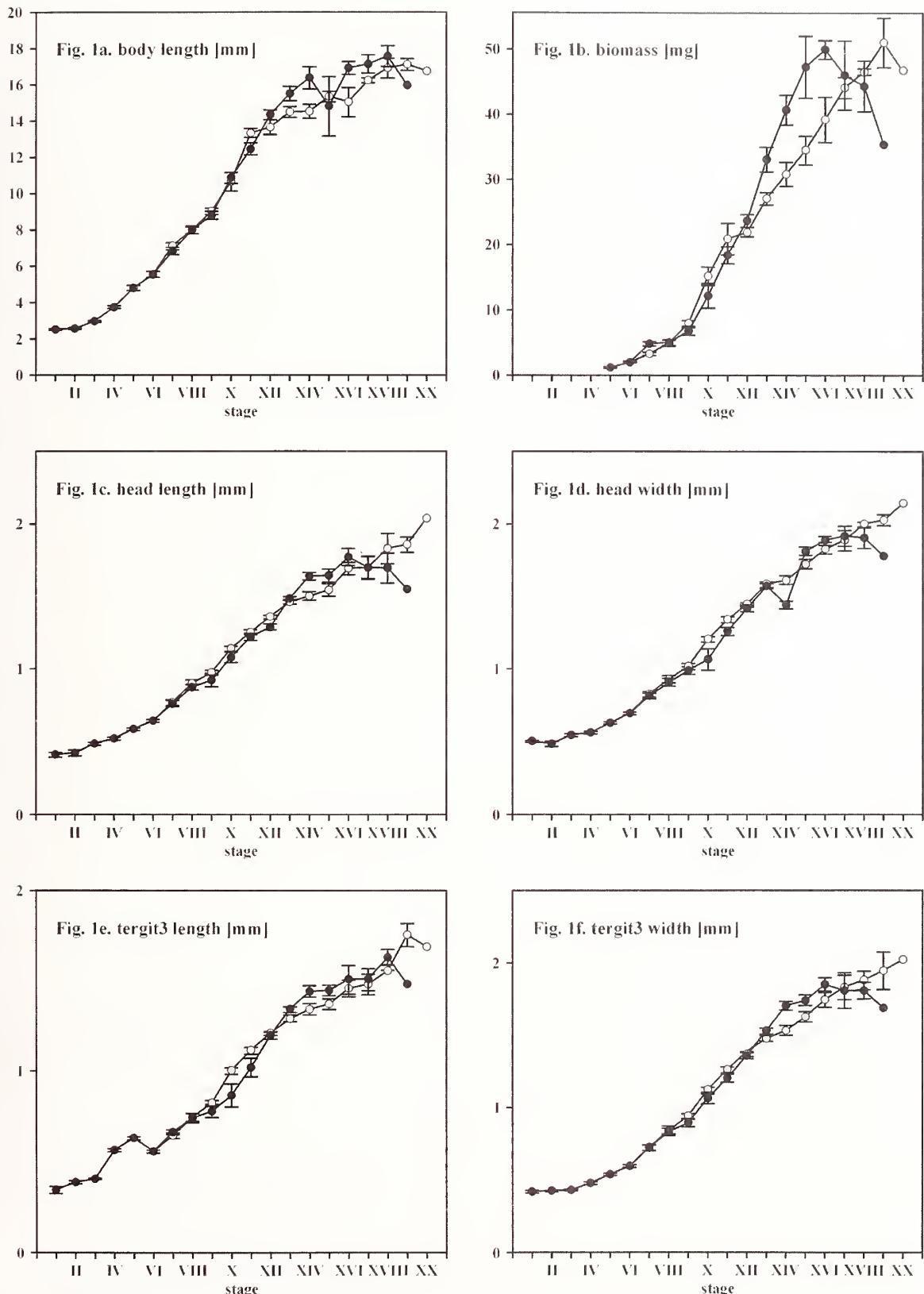


Fig. 1. Averages of body and biomass measurements of *L. mutabilis*. For numbers of measured specimens see Table 1; grey circles: males; black circles: juveniles and females.

Table 2. Comparison of different characters in epimorphic stages of *L. mutabilis* in the investigations from Neiße Valley (NV, present investigation), Steigerwald (St, FRÜND 1982) and Solling (So, ALBERT 1982).

| Stage | Sum of coxal pores of the leg pairs 12–15 | | | Antennal articles | | | Number of ocelli | | Head-width in mm | | | Body length in mm | |
|---------|---|----|----|-------------------|--------|-------|------------------|----|------------------|------|------|-------------------|--|
| | NV | St | NV | St | So | NV | St | NV | St | So | NV | So | |
| VI(1) | min. | | | 18 | 24 | 22 | 3 | | 0.57 | 0.58 | 0.66 | 4.13 | |
| | mode | 8 | 8 | 24 | 25 | | 5 | 5 | 0.69 | 0.70 | 0.75 | 5.63 | |
| | max. | | | 26 | 26 | 32 | 6 | | 0.83 | 0.74 | 0.88 | 7.09 | |
| VII(2) | ♂j | ♀j | | | | | | | | | | | |
| | min. | 8 | 8 | 8 | 24 | 26 | 24 | 4 | 5 | 0.67 | 0.78 | 0.76 | |
| | mode | 12 | 16 | 11 | 28, 29 | 28 | | 6 | 6 | 0.82 | 0.83 | 0.91 | |
| VIII(3) | max. | 16 | 16 | 16 | 34 | 30 | 33 | 8 | 7 | 0.98 | 0.89 | 1.10 | |
| | min. | 14 | 16 | 13 | 26 | 29 | 30 | 5 | 6 | 0.59 | 0.89 | 0.86 | |
| | mode | 18 | 20 | 18 | 31 | 31 | | 9 | 8 | 0.92 | 0.94 | 1.03 | |
| IX(4) | max. | 20 | 24 | 23 | 36 | 36 | 39 | 11 | 10 | 1.27 | 1.03 | 1.2 | |
| | min. | 18 | 18 | 19 | 31 | 35 | 33 | 5 | 9 | 0.85 | 0.92 | 1.06 | |
| | mode | 22 | 22 | 23 | 34, 35 | 38 | | 9 | 10 | 1.00 | 1.06 | 1.18 | |
| X(5) | max. | 22 | 26 | 28 | 39 | 43 | 39 | 10 | 12 | 1.17 | 1.16 | 1.34 | |
| | min. | 24 | 22 | 23 | 31 | 36 | 36 | 7 | 9 | 1.00 | 1.07 | 9.50 | |
| | mode | 28 | 28 | 27 | 40 | 41 | | 9 | 12 | 1.18 | 1.20 | 1.34 | |
| XI(6) | max. | 30 | 36 | 33 | 44 | 45 | 45 | 13 | 15 | 1.4 | 1.32 | 14.00 | |
| | ♂ | ♀ | ♂ | ♀ | | | | | | | | | |
| | min. | 26 | 28 | 28 | 33 | 28 | 40 | 10 | 11 | 0.96 | 1.23 | 9.73 | |
| XII(7) | mode | 32 | 34 | 32 | 37 | 39 | 43 | 12 | 14 | 1.31 | 1.35 | 1.47 | |
| | max. | 38 | 38 | 36 | 44 | 44 | 48 | 13 | 17 | 1.56 | 1.47 | 15.50 | |
| | min. | 30 | 30 | 28 | 35 | 30 | 40 | 9 | 13 | 1.07 | 1.35 | 11.14 | |
| XIII(8) | mode | 36 | 37 | 34 | 38 | 38–40 | 44 | 13 | 16 | 1.43 | 1.48 | 1.56 | |
| | max. | 42 | 44 | 39 | 43 | 45 | 48 | 18 | 20 | 1.63 | 1.57 | 17.5 | |
| | min. | 32 | 36 | 32 | 36 | 33 | 41 | 9 | 14 | 1.37 | 1.54 | 12.08 | |
| XIV(9) | mode | 38 | 42 | 36 | 40 | 39 | 43 | 13 | 18 | 1.58 | 1.61 | 1.65 | |
| | max. | 44 | 44 | 42 | 43 | 46 | 46 | 19 | 21 | 1.73 | 1.74 | 18.70 | |
| | min. | 34 | 38 | 37 | 45 | 33 | 40 | 12 | 19 | 1.46 | 1.64 | 13.63 | |
| XV(10) | mode | 40 | 46 | 40 | 48 | 39 | 44 | 14 | 21 | 1.69 | 1.72 | 1.76 | |
| | max. | 46 | 48 | 47 | 49 | 47 | 48 | 20 | 23 | 1.94 | 1.83 | 22.50 | |

to use the original terms of VERHOEFF (ANDERSSON 1976 ff.; FRÜND 1983; DAAS et al. 1996; SERRA & MIQUEL 1996; TUF 2002) and to call the anamorphic “larval” stages L0–L4, and the epimorphic “post larval” stages PL 1, PL 2, PL 3 etc. In the present study, the stages are designated (following DOHLE 1986) by Roman numerals from first to last stage (I–XX). Additionally, the epimorphic stages are numbered in parentheses with Arabic numerals [(1–15)].

A special problem was caused by ALBERT (1982) using the classification of stages created by VERHOEFF (1905) without consideration that VERHOEFF’s “agentilis” consists of two different stages (BRÖLEMANN 1930; JOLY 1966; LEWIS 1981). This mistake was corrected by ALBERT herself (ALBERT 1983b).

¹ The number most frequently is underlined..

Determination and number of stages. The anamorphic period of the post-embryonic development of *L. mutabilis* comprises five stages, each terminated by a moult. Easily discernible morphological characters distinguish each stage.

Stage I. Seven pairs of legs and one pair of unbristled limb buds (“Beinanlagen”). The buds of legs 9 can be seen as small lateral bumps at the end of the body. The number of ocelli and antennal articles is 2 and 7, respectively, in all individuals investigated (Figs 3, 4).

Stage II. Eight pairs of legs, but legs 8 are incompletely developed and non-functional. All individuals have 11 antennal articles and 2 ocelli.

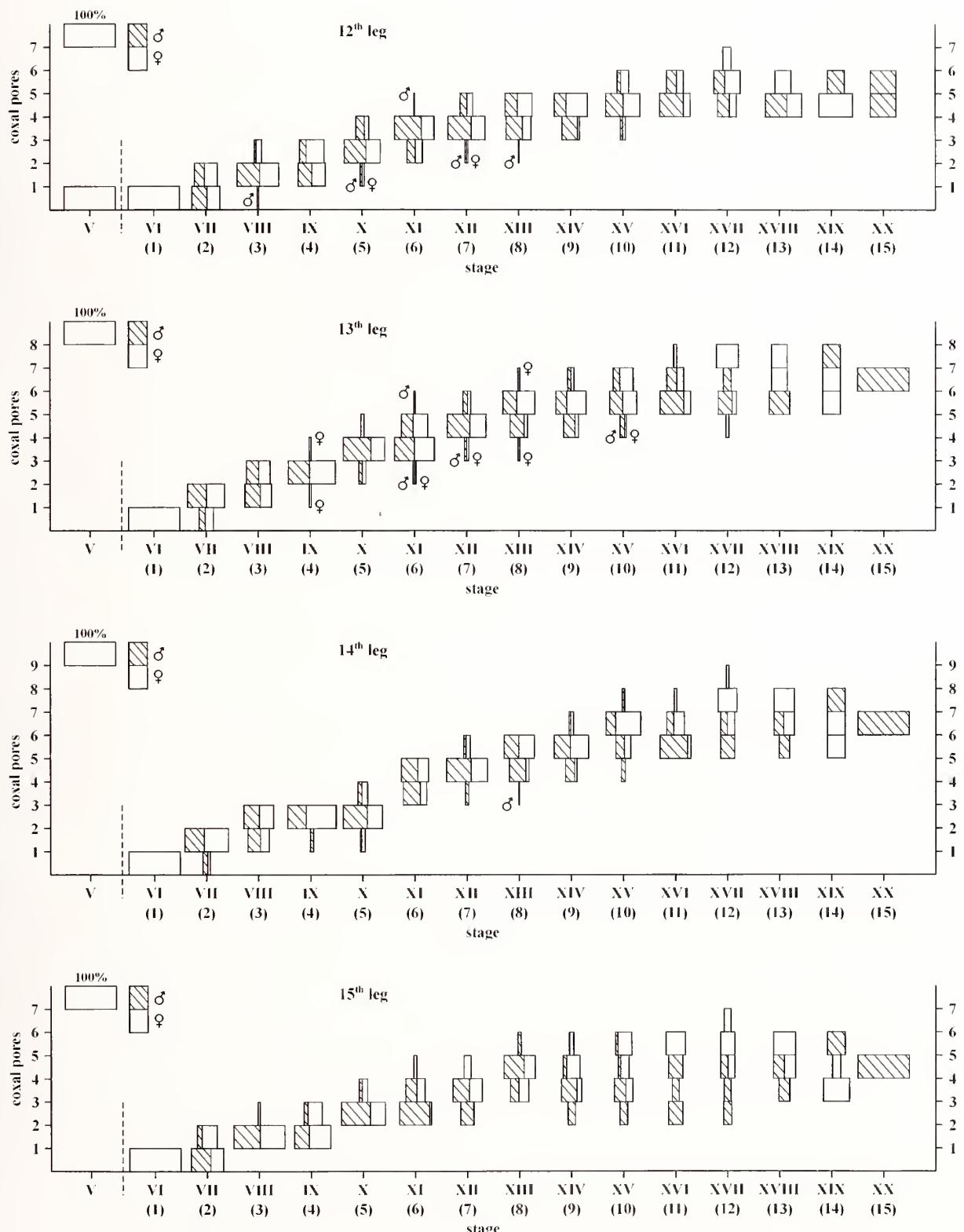


Fig. 2. Variation in numbers of coxal pores in different stages of *L. mutabilis*.

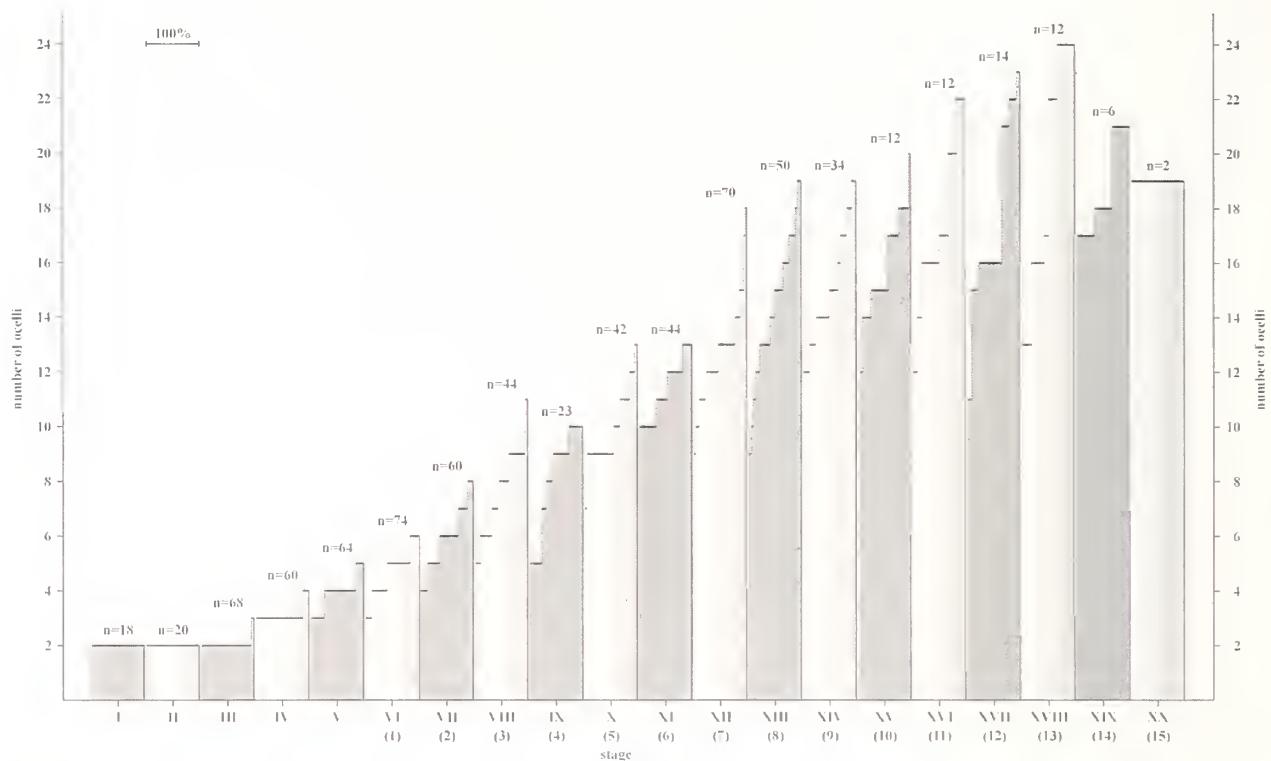


Fig. 3. Variation in numbers of ocelli in different stages of *L. mutabilis*, n: number of ocular fields counted.

Stage III. Eight fully developed pairs of legs and two pairs of limb buds; 14 antennal articles and 2 ocelli are characteristic for this stage. Very rarely 3 ocelli occur.

Stage IV. Ten pairs of legs and two pairs of limb buds. The number of antennal articles varies between 17, 18 and 19¹, the number of ocelli between 3 and 4.

Stage V (last anamorphic stage). Twelve pairs of legs and three pairs of limb buds, mostly with 23 antennal articles (16-23). The number of ocelli varies between 3, 4 and 5.

The first epimorphic stage VI (1) and all following stages have 15 functional pairs of legs. Therefore, other morphological characters (parameters of size as well as numbers of coxal pores, ocelli and antennal articles) must be used for determination of stages. The variability of these characters at each stage was determined for a better characterization of each stage.

The direct observation of all hatchings and the investigation of the development of different morphological characters during the life cycle of *L. mutabilis* in captivity led to the discovery of 15 epimorphic stages.

Growth analyses. The growth analyses show more or less

sigmoid curves (Fig. 1) for all parameters, especially for body length, head length and width, and width of tergite 3. Up to stage V (the last anamorphic stage), there is a relatively small increase between each moult. With the next stage VI (1), relatively constant greater increments appear (linear curves) up to approximately stage XIV (9), where the curves become flatter again.

The differences between various stages are highly significant for all measurements for males and females, whereas the differences between males and females of the same stage are very rarely significant (Mann-Whitney-U test).

Number of coxal pores. The last anamorphic stage V of *L. mutabilis* has one coxal pore on its last leg (leg 12; Fig. 2). The following epimorphic stages have pores at the coxae of legs 12-15. Each moult can lead to an increase of 1 or 0 coxal pores per leg. On leg 12 there is never an increase of pores during the moult from stage V to stage VI (1). From 273 observed epimorphic moults only 6 (2%) occurred without any addition of pores at one of the four pairs of coxae. Figure 2 shows the combination of coxal pores in different stages and sexes of *L. mutabilis*.

Females have more coxal pores than males (Table 2). Figure 2 shows that the differences between the sexes are due

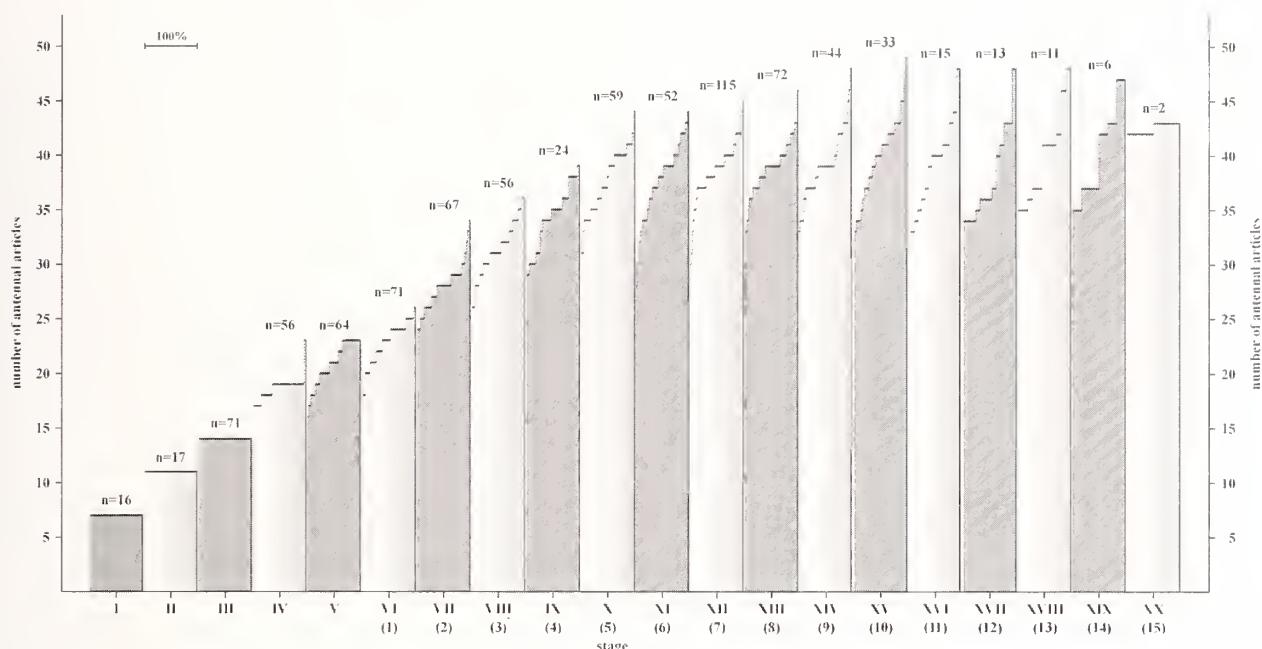


Fig. 4. Variation in antennal articles on each side in different stages of *L. mutabilis*, n: number of antennae counted.

to the lower number of coxal pores especially of leg 15 of males. In each stage there are certain preferred arrangements of increase. Overlaps of the preferred variants in males were between VIII (3) and IX (4), in females already between VII (2) and VIII (3). However, such overlaps apply to two stages only. In 16 % the left and right sides were different, but at most in one pore and on one leg only.

Number of ocelli. The first three stages have two ocelli on each side of the head. From stage IV onwards, the number of ocelli increases with each moult (Fig. 3). Variations begin with the (anamorphic) stage IV and become greater in later epimorphic stages. Within one stage, they can amount to as much as 12 ocelli. Thus, the overlap between different stages is very high. In both sexes, stage XVIII (13) with 24 ocelli has the highest observed number. The single male in the highest stage [XX (15)] had only 19 ocelli. No significant differences exist between males and females. Differences between the two sides of the head were rarely observed.

Number of antennal articles. The number of antennal articles increases during post-embryonic development from 7 to a maximum of 49 (Fig. 4). In the first three stages there is no variation in number. All studied antennae show

7, 11 or 14 articles, respectively. In stage IV, most individuals have antennae with 19 articles (with little variation). Beyond stage V, the number of antennal articles varies very widely within one stage. Also the left-right variability is very high (more than 50 %). In field-sampled individuals, it is often impossible to know whether a lower number results from an incomplete regeneration after loss of some articles.

In the first epimorphic stage VI (1), the usual numbers are 20 - 24 - 25. The increase continues up to stage X (5), after which it ceases (Fig. 4, Tab. 2). There is no significant difference in the number of antennal articles between males and females in any stage.

3.2. Reproduction biology and life cycle

Mating behaviour, oviposition and egg development. Mating behaviour and spinning of webs with spermatophores by males, as described by KLINGEL (1960) and DEMANGE (1956) for the species *L. forficatus* and *L. piceus gracilatarsus* Brölemann, 1898, were not observed for *L. mutabilis* in this investigation.

Of 57 adult females, 26 (both from the field and from laboratory cultures, investigated between 1993 and 1997) laid

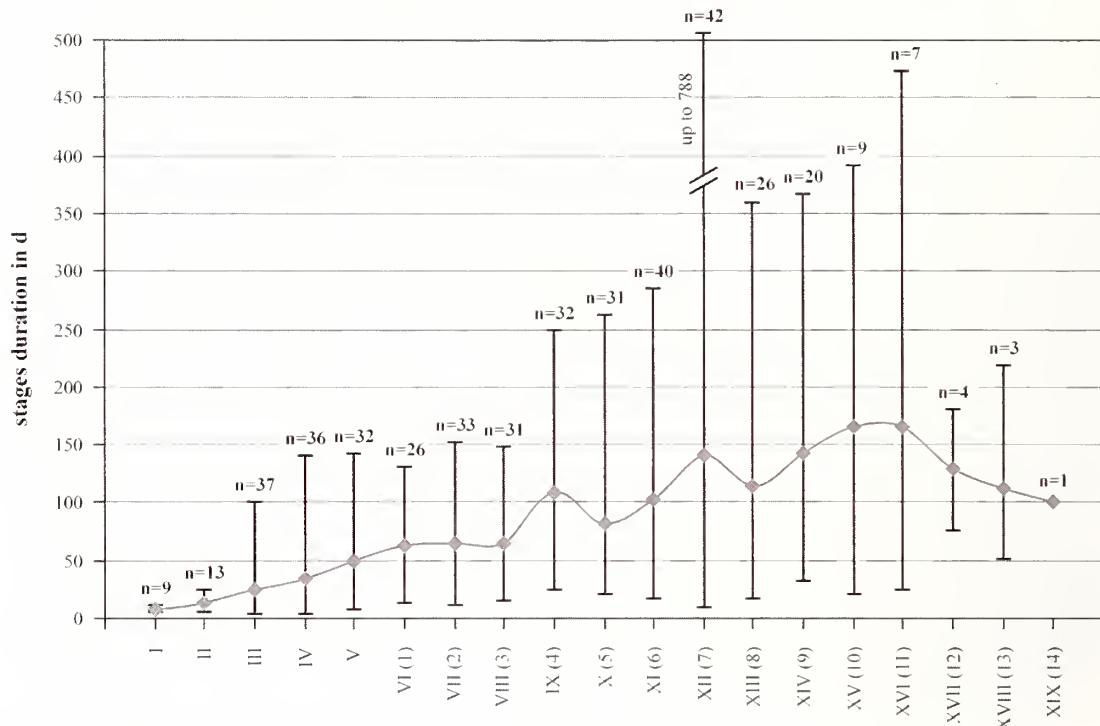


Fig. 5. Average stage duration, minimum and maximum of *L. mutabilis* [in days].

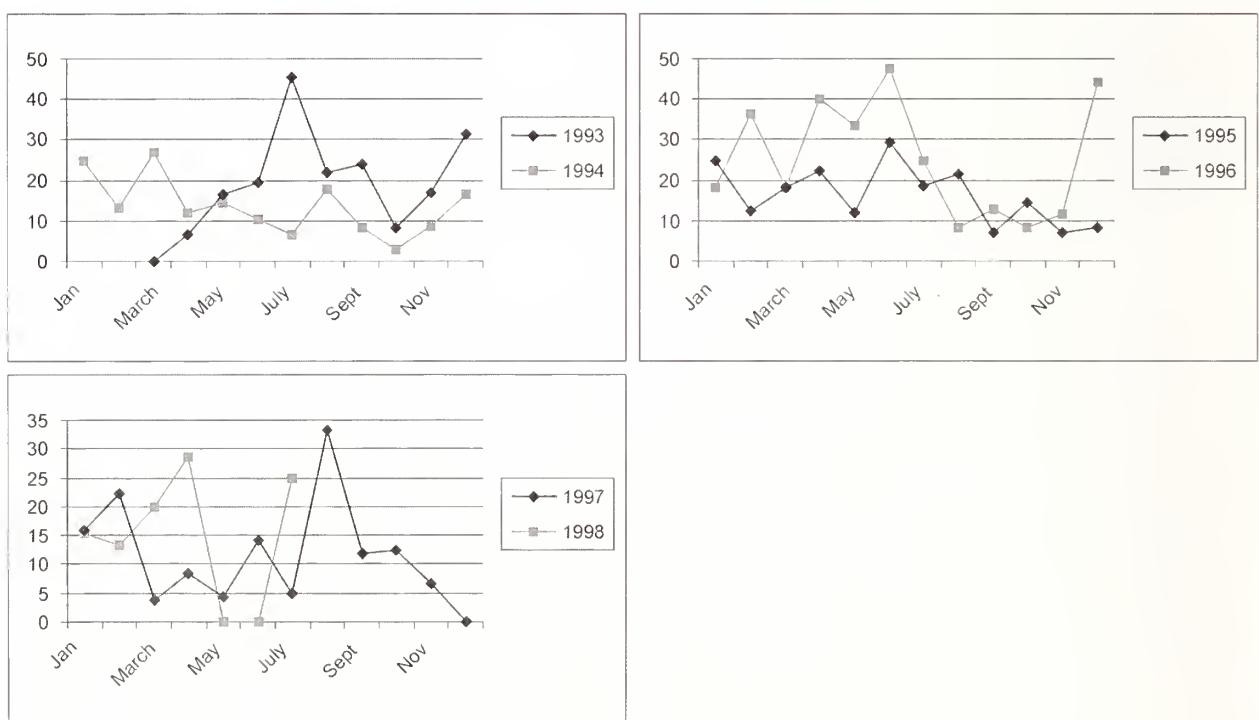


Fig. 6. Moulting activity of *L. mutabilis* in laboratory under constant conditions during the years 1993 to 1998 in % of the total number each month.

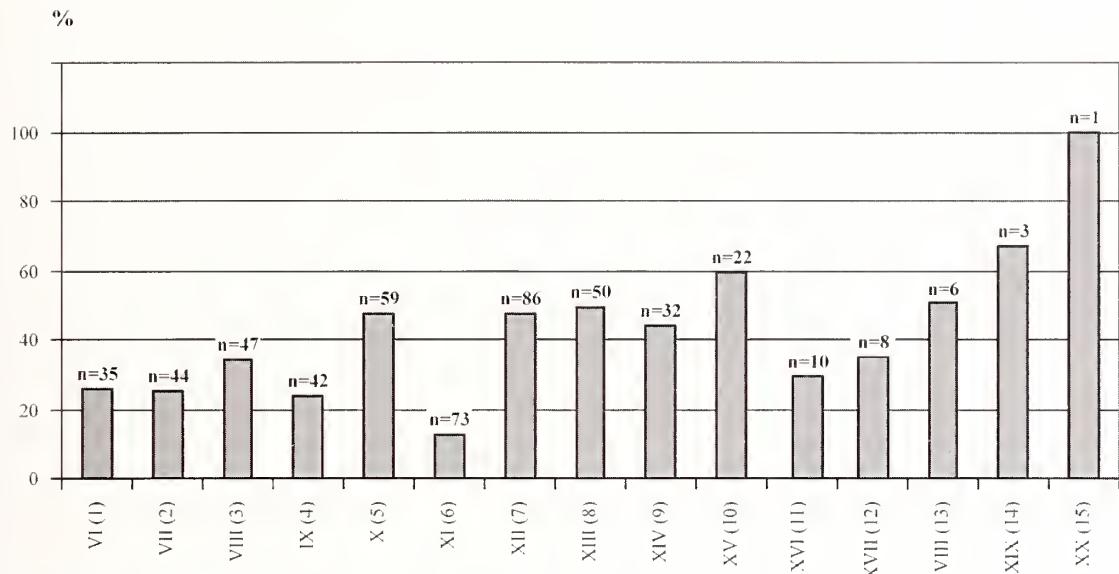


Fig. 7. Mortality rate of epimorphic stages of *L. mutabilis* in % of the total number in these stages.

eggs in captivity, some of them in several successive stages and in several years. Altogether 35 egg laying “periods” were observed by females of stages XI (6) to XVII (12). Egg numbers vary between 1 and 35, on average 11 eggs per female per egg laying period.

The eggs are laid singly. There is no maternal care of the brood in *L. mutabilis* as in other lithobiid species. The only protection for the eggs is a thin cover of fine soil particles, which is applied to the eggs by the female. In the rearing boxes without soil, this behaviour is retained and fine gypsum dust is used by the females. The egg laying itself and the following processes (BROCHER 1930 and SERRA & MIQUEL 1996 described it in detail for *L. forficatus* and *L. pilicornis*) could not be observed directly in this study. Only the covered eggs and females carrying eggs with their gonopods could be confirmed.

The eggs of *L. mutabilis*, as in other lithobiid species, are spherical and whitish. The mean diameter is 0.89 mm. The appearance of the youngest stages in nature (Neiße Valley) suggested that oviposition is not connected with a definite time in the year. This was also established by laboratory cultures of *L. mutabilis* in the present study. From 1/3 of laid eggs, young *L. mutabilis* were hatched. Though all eggs were kept under the same constant conditions (16 °C), they needed quite different times for their development. The time between oviposition and hatching ranged between 21 and 284 days (9.5 months). Most individuals hatched after 3-4 months.

Onset of sexual dimorphism and maturity. The sexes of *L. mutabilis* can be distinguished for the first time (with

some uncertainty) in stage VII (2), definitely in stage VIII (3). In the laboratory, first egg layings were observed in stage XI (6). Thus XI (6) can be seen as the first mature stage for females.

Duration of stages and moulting activity. The data for the duration of the different stages in the postembryonic development of *L. mutabilis* come from 150 specimens, both laboratory-reared as well as freshly captured. Some 490 moults were observed, 2–11 per individual. Observation of moults every two days was sufficient to ensure accuracy. If moults were not observed directly, at least the remains of exuviae were found. If they were completely eaten by moulted individuals, they could be seen in the faeces.

The mean stage duration increases with stage number (Fig. 5), but with higher variability in older epimorphic stages caused by some “slow” or “fast” individuals. It varies from only a few days to about 500 days. An extreme case was found in stage XII (7). Here, the shortest and longest duration was 10 and 788 days, respectively. The mean duration of stages XVII (12) to XIV (14) is based on only 1–4 animals and is therefore not representative.

However, it was not usual that a specimen had exclusively long (or short) durations of all the stages throughout its life. Therefore, it is possible to make general conclusions about the most important data based upon the average of stage duration (Figs 5, 8). In *L. mutabilis* the first epimorphic stage is reached after 4.5 months and sexual maturity is attained at the earliest after 1.5 years, definitely after 2 years. The maximal life expectancy is about

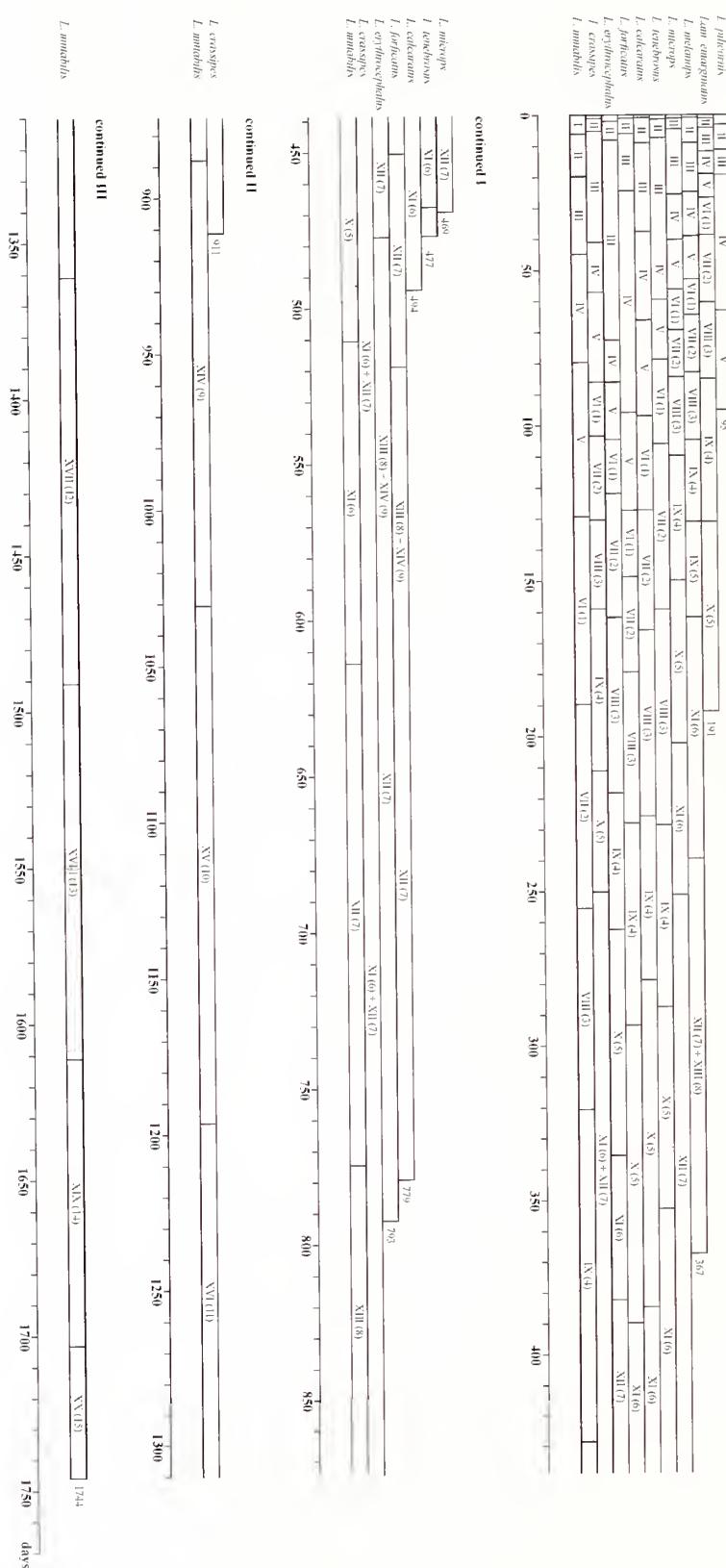


Fig. 8. Duration of developmental stages of different Lithobiomorpha (according to ANDERSSON 1990) and *L. mutabilis* (this investigation). For *L. pilicornis*, SERRA & MIQUEL (1996) give only data until stage V.

5 years. On average, *L. mutabilis* lives 3–3.5 years.

The moulting activity of the epimorphic stages of *L. mutabilis* during the years 1993–1998 can be seen in Figure 6. On average, 27 individuals per month were available. Under constant culture conditions, moults in *L. mutabilis* take place throughout the entire year without any peaks at a specific time.

Mortality. The mortality rate of 213 individuals of the epimorphic stages VI (1) to XX (15) was established. Figure 7 shows the number of dead individuals as a percentage of the total number in these stages. The values are not fully correct, because freshly collected and “laboratory” individuals were analysed together. It is possible that fresh individuals were more viable. Nevertheless, the mortality of the youngest epimorphic stages until XI (4) was very low. The transition from stage X (5) to XI (6), the first mature stage, was only reached by 50% of the individuals. In stage XI (6) the mortality was very low, but then it increased very rapidly. Most of the specimens died in stages XII (7) to XV (10). Only 11 individuals reached stage XVI (11) and only one the highest stage XX (15).

3.3. Observation and discussion on feeding behaviour

Some observations on the feeding behaviour were undertaken in the laboratory. They are compared with results of PFLEIDERER-GRUBER (1986) and ALBERT (1983a). These authors studied feeding behaviour more intensively in various centipede species, including *L. mutabilis*, in regard to prey capture, prey spectrum and preference, influence of different food resources on growth, and others.

Animal food. In the laboratory cultures, I offered different animal foods separately to *L. mutabilis* and other species at different time periods. Small pieces of earthworms and living *Tubifex* were given, as well as aphid larvae, small Diptera larvae and also *Collembola*. The choice of prey depended on the size relationship between predator and prey. Small collembolans (*Folsomia* spec.) were only attacked by juveniles of *L. mutabilis* and smaller species of the subgenera *Monotarsobius* and *Sigibius* [*L. austriacus* (Verhoeff, 1937), *L. microps*]. They noticed the prey only when their antennae came into direct contact with it. The observed feeding process is in correspondence with the description by RILLING (1968).

Minced meat was refused, contrary to results from PFLEIDERER-GRUBER (1986), who found it to be eagerly taken after 14 days of food withdrawal. Particularly bad results were experienced with ox heart. It led to a mass occurrence of mites (Heterocerconids) in the rearing vessels.

Their nymphs attacked the *Lithobius* species so massively, that they could not feed or were unable to move.

Cannibalism. *Lithobius mutabilis* was never observed to feed on members of the same species during the entire investigation period of more than 5 years, provided that the individuals had approximately the same size and were not injured. Once, a *L. forficatus* was observed attacking a defenceless specimen of the same species during moulting. The specimen bit at first in the “neck”, fed then on softer interior substances before eating pieces of the integument.

Plant food. In my investigations, I always offered green leaf pieces of indoor plants in addition to other food. In most cases, these plant pieces were clearly nibbled off.

According to PFLEIDERER-GRUBER (1986), all Chilopoda are pure carnivores and never eat plant material, detritus or soil, in contrast to other literature (e.g. DOBRORUKA 1961). PFLEIDERER-GRUBER assumed that such particles, which were only found as gut contents, were accidentally picked up with other food, or it could be still undigested gut contents of herbivorous prey. ALBERT (1983a) also writes that *L. mutabilis* does not seem to be able to feed on litter, even in times of food shortage.

My investigation refutes these doubts, at least in the case of *L. mutabilis*, which is able to bite off plant parts as food in small amounts. Therefore, it can be assumed that this species also can take in vegetable food under natural conditions.

4. DISCUSSION

4.1. Character analyses

Growth analysis. The growth of body parameters shows sigmoid curves corresponding to the two types of development: after a slow beginning during the first five anamorphic stages, linear growth rises more rapidly after the onset of epimorphic development. Then, stages XIV (9) to XX (15) seem to grow more slowly than the younger stages. However, this may be a result of the low number of individuals studied. An approximately linear growth of the body parameters of epimorphic stages is also found for many other *Lithobius*-species (ALBERT 1982; ANDERSSON 1976–1984; KOS 1997; VOIGTLÄNDER 2000). It seems to be typical for all Lithobiomorpha.

In millipedes, maturity often causes a cessation of growth because all reserves are used for the development of eggs and sperm (e.g., VOIGTLÄNDER 1987, 1996). This could not be established for *L. mutabilis* in the present in-

Table 3. Lithobiomorpha with investigated life cycles (or at least some aspects of it). * = examples for detailed descriptions of immature stages

| TAXON | AUTHOR(S) |
|---|---|
| <i>Arenobius mauegitus</i> (Chamberlin, 1911) | CHAMBERLIN (1917)* |
| <i>Bothropoly asperatus</i> (L. Koch, 1878) | MURAKAMI (1958) |
| <i>Esastigmatobius longitarsis</i> Verhoeff, 1934 | MURAKAMI (1960d) |
| <i>Ethopoly xauti</i> (Wood, 1863) | CHAMBERLIN (1925b)* |
| <i>Eupolybothrus nudicornis</i> (Gervais, 1837) | DAAS et al. (1996) |
| [Syn. <i>E. elongatus</i> (Newport, 1849)] | |
| <i>Eupolybothrus grossipes</i> (C.L. Koch, 1847) | EASON (1970)* |
| <i>Launyctinus coeculus</i> (Bröleemann, 1889) | ANDERSSON (1979, 1990) |
| <i>Lamyctes emarginatus</i> (Newport, 1844) | ANDERSSON (1979, 1984b, 1990), ZULKA (1991) |
| [Syn. <i>L. fulvicornis</i> Meinert, 1868)] | |
| <i>Lithobius atkiusoni</i> Bollman, 1887 | CHAMBERLIN (1925a)* |
| <i>Lithobius austriacus</i> (Verhoeff, 1937) | VOIGTLÄNDER 2000 |
| <i>Lithobius borealis</i> Meinert, 1868 | ANDERSSON (1979, 1980a, 1990) |
| <i>Lithobius b. burzelanicus</i> Verhoeff, 1931 | MATIC & STENTZER (1978) |
| <i>Lithobius calcaratus</i> C. L. Koch, 1844 | ANDERSSON (1979, 1982a, 1990) |
| <i>Lithobius canaliculatus</i> Murakami, 1963 | MURAKAMI (1963) |
| <i>Lithobius crassipes</i> L. Koch, 1862 | ANDERSSON (1979, 1981, 1990), WIGNARAJAH (1968) |
| <i>Lithobius curtipes</i> C. L. Koch, 1847 | ALBERT (1982, 1983b), ANDERSSON (1979, 1983, 1990) |
| <i>Lithobius dentatus</i> C. L. Koch, 1844 | VOIGTLÄNDER 2000 |
| <i>Lithobius erythrocephalus</i> C. L. Koch, 1847 | ANDERSSON (1978b, 1979, 1990), VOIGTLÄNDER (2000) |
| <i>Lithobius forficatus</i> (Linné, 1758) | CHAMBERLIN (1925a)*, VERHOEFF (1925), BROCHER (1930), LEWIS (1965), WIGNARAJAH (1968), ANDERSSON (1976, 1979, 1990) |
| <i>Lithobius hirsutipes</i> Eason, 1989 | EASON (1989)* |
| <i>Lithobius lapidicola</i> Meinert, 1872 | ANDERSSON (1980a) |
| <i>Lithobius macileucus</i> L. Koch, 1862 | ANDERSSON (1990) |
| <i>Lithobius melanops</i> Newport, 1845 | ANDERSSON (1979, 1980b, 1990) |
| <i>Lithobius microps</i> Meinert, 1868 | ANDERSSON (1979, 1982b, 1990), VOIGTLÄNDER (2000) |
| <i>Lithobius mutabilis</i> L. Koch, 1882 | ALBERT (1982, 1983b), FRÜND (1983) |
| <i>Lithobius nihamensis</i> Murakami, 1960 | MURAKAMI (1961) |
| <i>Lithobius obscurus azoreae</i> Eason & Ashmole, 1992 | EASON & ASHMOLE (1992)* |
| <i>Lithobius pachypedatus</i> Takakuwa, 1938 | MURAKAMI (1960a, b, c) |
| <i>Lithobius peregrinus</i> Latzel, 1880 | Barber & Eason (1986)* |
| <i>Lithobius piloricus</i> Newport, 1844 | SERRA & MIQUEL (1996) |
| <i>Lithobius schawalleri</i> Eason 1989 | EASON (1989)* |
| <i>Lithobius tenebrosus femoscaudicus</i> Lohmander, 1948 | ANDERSSON (1984a, 1990) |
| <i>Lithobius punctulatus</i> C. L. Koch, 1847 | Kos (1997) |
| [Syn. <i>L. validus</i> Meinert, 1872] | |
| <i>Lithobius variegatus</i> Leach, 1814 | ROBERTS (1957), EASON (1964)*, LEWIS (1965) |
| <i>Nothebius insulae</i> Chamberlin, 1916 | CHAMBERLIN (1916)* |
| <i>Oabis pylorus</i> Chamberlin, 1916 | CHAMBERLIN (1916)* |
| <i>Paobius boreus</i> Chamberlin, 1916 | CHAMBERLIN (1916)* |
| <i>Tidabius tivius</i> (Chamberlin, 1909) | CHAMBERLIN (1913)* |

vestigation. In spite of the early maturity, at stage XI (6), this species still grows continuously in all measured parameters. Corresponding results were published by FRÜND (1983) (head width) and ALBERT (1982) (body length, head width) for *L. mutabilis*.

Coxal pores. In all Lithobiomorpha, the first coxal porus is developed on the leg 12 in stage V already, whereas the coxal pores of legs 13–15 appear in stage VI (1) at first. The present investigation corroborates this for *L. mutabilis* (Fig. 2). In contrast to other species (e.g., *L. erythrocephalus*, *L. melanops*, *L. crassipes*, *L. curtipes*), where two pores may be observed on leg 12 of stage VI (1) (ANDERSSON 1978b, 1980b, 1981, 1983), for *L. mutabilis* only one coxal pore was found in all individuals of stage VI (1).

As a general rule for Lithobiomorpha shown in many investigations (Tab. 3), no more than one coxal pore per leg is added during a moult. For this reason, the number of pores of legs 13–15 does not exceed the number of the epimorphic stage; rarely it is the same at least. Only on leg 12, one more coxal pore is possible, because one pore is already developed in stage V. Therefore, the number of coxal pores is a very good character for separating the different stages of *L. mutabilis*, just as in other *Lithobius*-species.

For some species, e.g., *L. calcaratus*, *L. crassipes*, *L. curtipes* (ANDERSSON 1981, 1982a, 1983), *L. piceus* and *L. tricuspidis* (TOBIAS 1969), it was established that coxal pores are more numerous in females than in males. This is also valid for *L. mutabilis*.

Neiße Valley- and Steigerwald-populations show approximately the same numbers of coxal pores summarized from the last four legs in minimum, maximum and “mean” (Tab. 2). The “mean” values differ only by 1–2 (3) pores. The differences between minimum values and maximum values, respectively, are a little higher (up to 7 pores). In both studies, females had significantly more coxal pores than males.

If a comparison between the coxal pores of each leg is made, a very close similarity between the populations can also be seen (Fig. 3 herein and fig. 2 in FRÜND 1983). Not only are the numbers of pores on each leg the same in comparable stages, but also the distribution of the numbers. In both studies, legs 13 and 14 reach the most (7) coxal pores. In the present investigation, the number of coxal pores increases to 8 or 9 in later stages, not found by FRÜND (1983).

If ALBERT’s (1982) PL1 consists of two different stages, then the number of coxal pores is similar to FRÜND’s and the studies presented here.

Ocelli. In the investigations at Steigerwald (FRÜND 1983), variations in the number of ocelli begin in stage VI (2) (Tab. 2), whereas in the present study they start during anamorphic development in stage IV (Fig. 3). However, in stage VI (1) the usual number was 5, as in the Steigerwald-population. The increase of the number of ocelli was more regular in the investigations by FRÜND (1983) than in the presented study, where some successive stages show the same number of ocelli on average.

The increase of ocelli during post-embryonic development of *L. mutabilis* shows more or less the same pattern as in other *Lithobius*-species. With the exception of *L. forficatus*, *L. variegatus* and *L. pilicornis*, all species investigated up to now have two ocelli in the first three anamorphic stages. Then a more or less linear increase can be observed. However, in higher stages, a greater variability in increase of ocelli number occurs. Differences between the sexes do not exist in all *Lithobius* species, and irregularities between the left and right side are rare.

Antennal articles. In the present investigation, a gradual increase in the mean numbers of antennal articles is only seen until stage X (5). However, in the population from Steigerwald (FRÜND 1983) this cessation in increase occurs later [XI (6)]. The numbers reached in the different stages are mostly smaller in the present investigation and some differ very much from those observed by FRÜND (1983) (Table 2). The variations within stages are larger, as is the overlap between different stages. Altogether, the growth of antennae in the population from Steigerwald is more regular than in that of the Neiße Valley-population. The numbers of antennal articles of specimens from Solling (ALBERT 1982) show also high variation, especially in the younger stages (Tab. 2).

In comparison with other Lithobiomorpha (ANDERSSON 1976–1984), there are no differences for the first three anamorphic stages. In later stages of *Lithobius*, the increase takes place in two different ways. In some species (*L. melanops*, *L. calcaratus*, *L. tenebrosus fennoscandicus*), the increase continues until the last stage almost in linear fashion. In others (*L. microps*, *L. erythrocephalus*, *L. forficatus*), the growth of antennae is almost completed at a specific stage [IX (4), X (5), XI (6) or XII (7)]. To this group belongs *L. mutabilis* [stagnation from X (5)].

Characteristically for all *Lithobius*-species (including *L. mutabilis*) is the absence of differences in the number of antennal articles between males and females. The extensive variation in the number of antennal articles within a stage in all species is also typical, but may partly result from undetected regeneration. Therefore, the use of this character for stage determination is restricted.

4.2. Number of stages

Like all Lithobiomorpha, *L. mutabilis* develops by hemianamorphosis with five anamorphic and a various number of epimorphic stages. VERHOEFF (1905) described only five epimorphic stages for *L. mutabilis* and called them "status agentilis" (realized by BRÖLEMANN [1930] and JOLY [1966] as "agentilis I" and "agentilis II"), "status imaturus", "status praematurus", "status pseudomaturus" and "status maturus". ALBERT (1982) and FRÜND (1983) distinguish nine epimorphic stages.

How can differences in the number of observed stages come about? ALBERT (1982) and FRÜND (1983) almost exclusively investigated animals that were collected in the field. Only a few individuals were reared for testing in the laboratory. It is impossible to determine the exact epimorphic stage of field animals, because the range of variation of all characters used for stage determination is very large and overlaps between stages. Only direct observation of moulting in the laboratory makes it possible to determine the correct number of stages. Additionally, most individuals die in stages XIII (7) to XV (10), even under favourable conditions in the laboratory (Fig. 6). Thus, it is conceivable that, in the field, death happens even earlier. FRÜND (1983) sampled most individuals at stages X (5) to XII (7). In the Neiße Valley more than half of all sampled individuals were found to be stages XI (6) and XII (7). Later stages were sampled very rarely (20%) in the Neiße Valley.

4.3. Life cycle

Oviposition. Oviposition in *L. mutabilis* is not connected with a certain time of year. This was established by laboratory cultures in the present study as well as by investigations of ALBERT (1979, 1983b). According to LEWIS (1965) and WIGNARAJAH & PHILLIPSON (1977), lithobiids are able to lay eggs during the whole year (*L. variegatus*), but some species (e.g., *L. forficatus*) have a main egg-laying period in spring and a smaller one in autumn. This different behaviour of the species and the small number of eggs laid during each oviposition period might be interpreted in correlation to habitat choice. A long egg-laying period guarantees a breeding success, even if some of the eggs are destroyed through unfavourable conditions, such as dryness. The behaviour of *L. variegatus* (LEWIS 1965) and *L. mutabilis* may indicate that they are less resistant to climatic extremes than *L. forficatus*. Both species live in woodland, whereas *L. forficatus* is more euryoecious and often prefers dry habitats.

A female *L. mutabilis* can lay eggs in several periods (each of these periods can reach up to two months), each sepa-

rated by one moult at least. In *L. forficatus* – as well as in some diplopods – the development of the eggs and moults is subject to mutual hormonal mechanisms of regulation (RICHTER 1967; SCHEFFEL 1969; LEUBERT & SCHEFFEL 1984; VOIGTLÄNDER 1987). The same mechanisms seem to control the life cycle of *L. mutabilis*.

Egg development. The present investigation shows a large variation in the duration of egg development. This agrees with other studies on *L. mutabilis*. ALBERT (1983b) ascertained individually variable developmental times between 27–269 days (15 °C) and TUF (2002) found time periods of approximately 150–200 days under natural conditions.

This different "hatching period" in combination with a long egg-laying period characterises the life strategy of *Lithobius* in general, not only of *L. mutabilis*. It guarantees the survival of at least some individuals.

Onset of maturity and insemination time(s). In agreement with the present results, ALBERT (1983b) also defined stage X1 (6) as first mature stage of *L. mutabilis*. FRÜND (1983) deduced from investigations of the structure of the secondary sex characters that X (5) is not yet adult, but stages XII (7) to XIV (9) definitely are.

To determine the first stage of maturity in males, it is necessary to examine the testes, i.e. whether they contain sperm. It is not possible to prove this in breeding cultures. Each female was kept with one or two males, but it is not certain whether their eggs were fertilized by the males present, because females are able to conserve sperm in their seminal receptacles for up to two years (personal observations on a lone female). The same phenomenon was found in Scutigeromorpha (MURAKAMI 1956, DOHLE 1969). TOBIAS (1969) observed egg laying in *Lithobius* seven months after isolation of the females and VERHOEFF (1915) after approximately one year. Personal observations support the period of one year for *L. forficatus*.

Individual development. The high individual variability of stage duration (Fig. 5) means that new developmental periods (epimorphic development, maturity) begin at very different times in each individual. Moult activity and stage duration depend to a large degree on the environmental conditions. Mostly food shortage and low temperatures inhibit development (ROBERTS 1957; JOLY 1977; ANDERSSON 1978a). The loss of extremities can stimulate moulting (VERHOEFF 1915; SCHEFFEL 1980).

Under constant temperature conditions and optimal feeding in the present study, it was expected that all individuals would have a relatively similar stage duration. But, on the contrary, they varied very widely especially in higher epimorphic stages. This is not only a phenomenon of

L. mutabilis, but occurs in other species too (ANDERSSON 1990).

However, the individual differences in stage duration in the studies of ANDERSSON, ALBERT, and myself cannot be caused by hunger, since all individuals were well fed in all investigations. Further, the different constant culture temperatures (ANDERSSON: 20 °C, ALBERT: 15 °C, present study: 16 °C) could have had an influence. But ANDERSSON investigated all species under the same conditions and also found large differences between the species additionally to the individual differences. Thus, it seems that environmental conditions have only a secondary influence on intra- and interspecific variability of life span.

To explain the interspecific differences ANDERSSON (1990) suggested the possibility of a “built-in clock” by inspection of moults in different months. The smaller (*Sigibius Monotarsobius*) species, *L. microps* and *L. crassipes*, show many fewer moults during the winter. The larger (*Lithobius* s.str.) species, *L. forficatus* and *L. erythrocephalus*, show no regular differences. Up to now, there is no explanation for the difference in moulting pattern between large and small species. The investigations have shown that *L. mutabilis* moults throughout the entire year under constant temperature conditions. It can thus be assumed that *L. mutabilis* does not have a “built-in clock”. This corresponds with the other larger *Lithobius*-species (ANDERSSON 1990).

Population development. The most important life history data for *L. mutabilis* from Neiße Valley are in concordance with those found for the Solling-populations by ALBERT (1983b). The author gave 0.5–1 year till attainment of stage VI (1) (4.5 months in the present paper). Maturity is reached earliest in stage X (5) after 1.5–2 years according to both investigations. The total life span in *L. mutabilis* is suggested by ALBERT’s abundances data to be between 4 and 7 years, which is a little longer than in the present study by laboratory observations (3–5 years).

Figure 8 shows the developmental time of different species (according to ANDERSSON 1990; SERRA & MIQUEL 1996) in comparison to *L. mutabilis* (present paper). The shortest stage of *L. mutabilis* was stage I with only 5 to 12 days, which is much longer than in all other investigated species. The first epimorphic stage was reached after 4 months, approximately the same time as in *L. forficatus*, but longer than in other species. *L. mutabilis* has reached stage XI (6) after 510 days only, whereas other species reach this stage as early as after 255–390 days (Fig. 8). This means a very retarded development of *L. mutabilis*. This species has the highest number of stages as well as the greatest age of all species investigated in the laboratory. However, it seems that *L. mutabilis* dies earlier in the field than in captivity.

4.4. Conclusions

The results of the character analyses (growth, biomass, number of coxal pores, antennal articles and ocelli) in the geographically widely separated populations of *L. mutabilis* Steigerwald, Solling (western Germany) and Neiße Valley (eastern Germany) show very high correspondence. The number of stages recognised in this laboratory study was much higher than in the other investigations, perhaps due to methodological problems of stage analyses on older field-collected individuals. However, the life cycles of the different populations are very similar. This suggests that in *L. mutabilis* the study of an isolated case can be generalised and this may also be true for other species.

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